**Quick guides**

# Electric fish

**Mark E. Nelson**

***What are electric fish?*** First of all, they don't run on batteries, or need a power cord. An electric fish is one that generates its own electric field using a specialized electric organ. Such fish are said to be *electrogenic*. Fish that have the ability to detect electric fields are said to be *electroreceptive*. Most electrogenic fish are also electroreceptive. In contrast, there are many electroreceptive fish species that are not electrogenic.

***How common are electric fish?*** Most bony fishes (teleosts), including many species you would find in a tropical fish store or at the local fish market, are neither electrogenic nor electroreceptive. Certain fishes like sharks, skates, rays and catfish can detect electric fields, and are thus electroreceptive, but they don't generate electric fields so they are not classified as electric fish. Although they can be very abundant in certain habitats, electric fish represent only a small fraction of all fish species: of the more than 30,000 total fish species, only about 350 are electrogenic.

***Can electric fish give you an electric shock?*** Some can and some can't. Those capable of generating a perceptible and possibly painful electric shock would be classified as strongly electric fish (Figure 1). Such fish use their electric discharge to stun prey and as a defensive mechanism. Scientists that work with strongly electric fish, like the electric eel, typically wear rubber gloves when handling the animals. In contrast, other electric fish generate very weak discharges that are used only for sensing the environment and for communicating with one another. Putting your hand in an aquarium with one of these weakly electric fish would not elicit even the slightest tingle.

***Where are they found?*** Some strongly electric fish are found in the oceans, including the electric stargazer, *Astroscopus*, and certain skates and rays, such as the torpedo ray (Figure 1). Other strongly electric fish are found in freshwater habitats, including the South American electric eel, *Electrophorus*, and the African electric catfish, *Malapterurus*. Most weakly electric fish are found in freshwater rivers of Africa and South America; some species of marine skates and rays are also weakly electric.

***How is the electric field generated?*** The electric field is produced by a dedicated electric organ, which is made up of modified nerve or muscle cells called electrocytes. So-called neurogenic electric organs arise from specialized axons originating in the spinal cord, while myogenic electric organs arise from transformed skeletal muscle, typically in the trunk region of the fish. Electrocytes employ mechanisms of electrical excitability similar to those of normal nerve and muscle cells. The externally measured electric field arises from the synchronized activation of thousands of electrocytes. For most electric fish, the electric organ is located in the tail. The output waveform is called the electric organ discharge. In some species, the electric organ discharge is continuous and almost sinusoidal; these fish are said to have a *wave-type* discharge. In other species, the electric organ waveform consists of brief pulses separated by longer gaps; these fish are said to have a pulse-type discharge (Figure 1).

***How did electric fish evolve?*** Electrogenic capability has evolved multiple times in both cartilaginous and bony fishes — at least eight times among the bony fishes (teleosts) alone. In almost all cases, it appears that passive electroreceptive capability was already present. Passive electroreception was an early evolutionary innovation that allowed fish to detect the weak, naturally occurring bioelectric potentials generated by other aquatic organisms. Evolution of electric organs probably originated with a set of highly active skeletal muscles that generated sufficient electrical activity to be detectable by the fish's own electroreceptors. The ability to monitor this self-generated field could provide a selective advantage by enhancing the fish's ability to navigate and communicate, particularly at night or in murky waters. Strong electric organs probably evolved as a subsequent specialization.

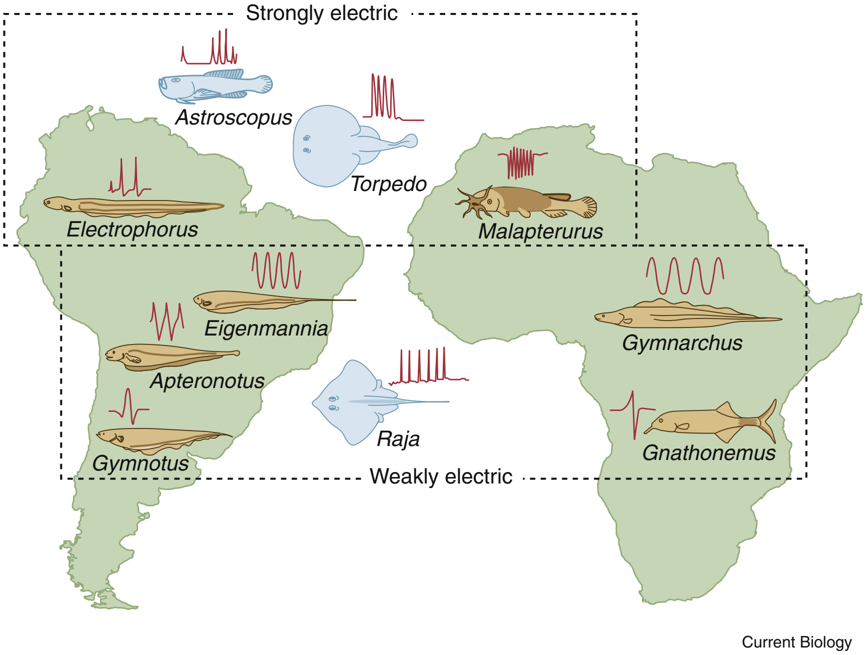

Figure 1. Types and distribution of electric fish.
Species of electric fish can be found in freshwater rivers of Africa and South America, as well as marine environments. Marine species are depicted in blue, freshwater species in yellow. Strongly electric fish use electricity to stun their prey, while weakly electric fish use electricity for sensing and communication. The waveform above each fish represents the time course of the electric organ discharge that would be recorded in the water near the fish. (Modified from Moller, P. (1995). Electric Fishes: History and Behavior (London: Chapman and Hall). With kind permission from Springer Science and Business Media B.V.)

***What is the electric field used for?*** Strongly electric fish have an electric organ discharge that is powerful enough to stun prey and to discourage potential predators. The brief, intermittent discharge pulses generated by strongly electric fish can range up to several hundred volts. In contrast, weakly electric fish generate a discharge that is typically less than a single volt. These discharges are too weak to stun prey, but are used for navigation, object detection (electrolocation) and communication with other electric fish (electrocommunication). These abilities are particularly useful since many electric fish are nocturnal and live in turbid waters.

***How are electric fields detected?*** The body of an electric fish is typically covered with thousands of specialized sense organs. Each electroreceptor organ consists of a small pit in the skin with a cluster of sensory cells in the bottom of the pit. The receptor cells act like miniature voltmeters and monitor the voltage drop across the skin. Objects near the fish alter the pattern of electric current flow across the skin, which changes the transdermal voltage measured by the sense organs. Electric fish analyze the spatial and temporal patterns of voltage change across the skin to detect and characterize objects in their environment and signals generated by other electric fish.

***How do strongly electric fish avoid getting electroshocked themselves?*** Strongly electric fish, such as electric eels, have layers of adipose and connective tissue that help electrically insulate their vital organs from the electric currents produced by their own discharge. Because electric currents tend to follow the path of least resistance, they tend to flow around, rather than through these higher resistance tissues. The protection isn't perfect, however. Electric eels are sometimes observed to twitch in response to their own discharge, presumably due to the involuntary electrical activation of muscle fibers or motor axons.

***What is the jamming avoidance response?*** Some electric fish have neural circuitry that prevents them from jamming each other's electric signals. Interference can arise when two nearby fish use similar discharge frequencies, much as it would if two nearby radio stations tried to broadcast on the same frequency channel. The jamming avoidance response adjusts the fish's discharge frequency to avoid interference with neighbors. Using sensory cues related to the amplitude and phase modulations of the interference pattern, two fish will reflexively shift their electric organ discharge frequencies away from one another if they are interfering. Neuroscientists have carefully worked out the neural circuits, coding strategies, and associated computations that underlie this remarkable ability, making it one of the most completely characterized sensorimotor behaviors in any vertebrate.

***Anything else we need to know about electric fish?*** Some electric fish can swim backwards using an unusual ribbon-fin propulsion system; this mechanism is being investigated as a means to create highly maneuverable aquatic robots. The pacemaker nucleus that controls the timing of electric organ discharges is one of the most temporally precise biological oscillators ever measured. Electric fish are very good at measuring small time differences — they can resolve disparities in the microsecond range. In some species, the electric organ discharge carries information about the sex and social status of the individual. Some electric fish serenade potential mates with exotic discharge patterns ('chirps', 'rasps' or 'creaks') during courtship. Electric fish tend to have large brain-to-body size ratios, leading to speculation that these are some pretty smart fish!

### *Where can I find out more?*

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# Desmosomes

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***What are desmosomes?*** Desmosomes are specialized adhesive protein complexes that localize to intercellular junctions and are responsible for maintaining the mechanical integrity of tissues. The term 'desmosome' was coined by Josef Schaffer in 1920 and has its origins in the Greek words for bond (*desmo*) and body (*soma*). Desmosomes are also known as *maculae adherentes*, which is Latin for 'adhering spot'. Unlike adherens junctions (AJs), which connect to the actin cytoskeleton network, desmosomal junctions are tethered to the intermediate filament network. Desmosomes appeared later than AJs during evolution, but, like AJs, desmosomes are necessary for life in vertebrates. Desmosomes have historically been considered static 'spot welds', but recent studies have uncovered important roles for desmosomes in a myriad of cellular functions, such as cell differentiation, cytoskeletal architecture, cell migration and gene expression.

***It's a pretty sticky business...*** A primary function of desmosomes is to form stable adhesive junctions between cells. Proteins from three main families coordinate to perform this function (Figure 1). Desmosomal cadherins, desmogleins (Dsgs) and desmocollins (Dscs), are transmembrane proteins that interact in the extracellular space to connect cells together. The extracellular and proximal intracellular domains of desmosomal cadherins share homology with classic cadherins, but desmogleins have unique, extended carboxy-terminal domains, the functions of which are still being elucidated. On the intracellular face, the armadillo proteins plakophilins (PKPs) and plakoglobin (PG) form an extensive network of interactions between themselves and other desmosomal components, thus providing lateral stability to the complex. PKPs and PG have central armadillo repeats like their AJ orthologs, p120 catenin and β-catenin; however, all known